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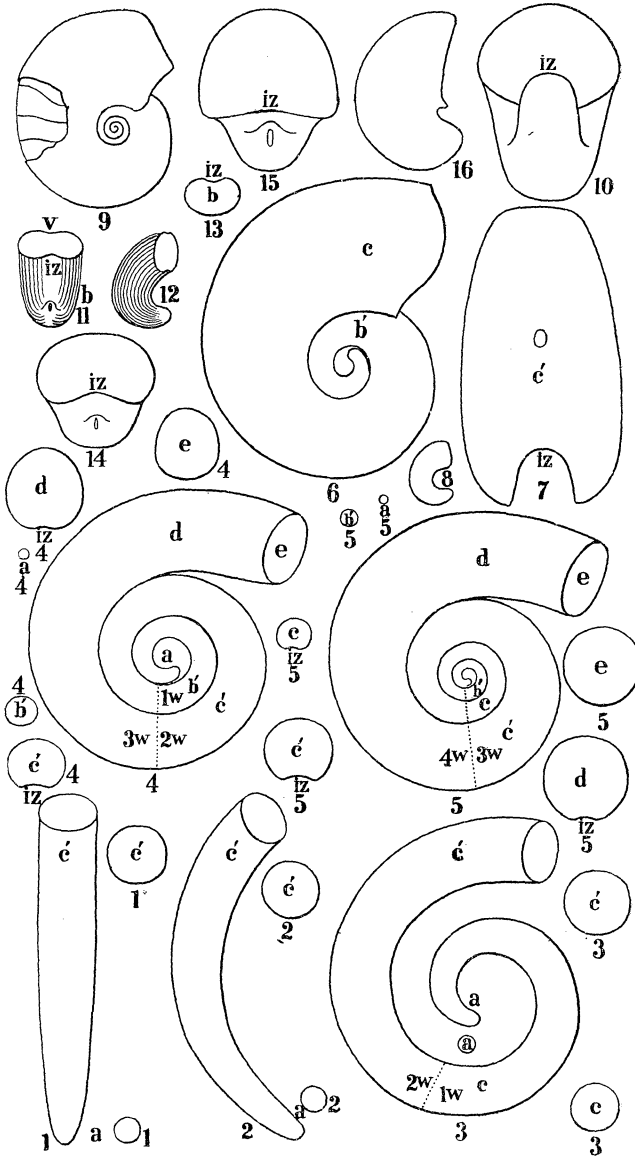
# PLATE XVIII.




Hyatt on Cephalopoda.

# PHYLOGENY OF AN ACQUIRED CHARACTERISTIC.

By Alpheus Hyatt.

An acquired character is a modification which makes its appearance in the adult or later stages of development and is obviously dependent for its origin upon other than hereditary causes. I have elsewhere defined that branch of science which deals with such problems as Ctetology and such characters as ctetic or acquired. The characteristic dealt with in the paper of which this is an abstract, is of essential importance among Nautiloids and Ammonoids or all of the Cephalopoda having chambered shells and living within their shells. It consists mainly of an impression made on the inner side or dorsum of each outer whorl during the coiling up, as the whorl grows and is moulded over the venter or outer side of the next inner whorl.

This matter will be better understood, if a short description is given of the following figures. Figs. 1–2 show an almost

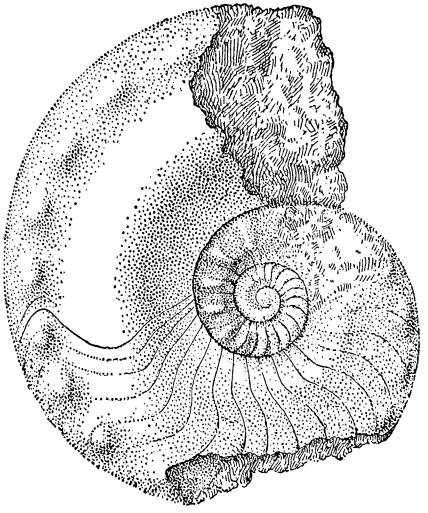


Fig. 1.

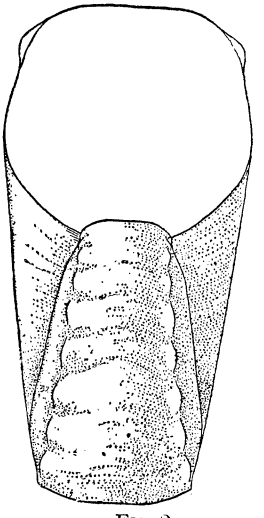


Fig. 2.

complete fossil cast of a full grown *Metatoceras cavatiformis* Hyatt, and some of the lines or sutures made in the external surface of the cast by the intersections of the partitions or septa that cut up the coiled tube of the living shell into air chambers. Figs. 3–4 show a broken specimen of the same

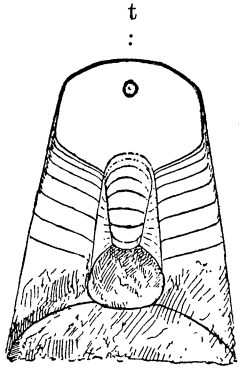



FIG. 3.

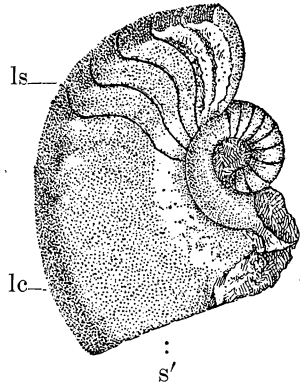



FIG. 4.

species, but with the outer and older whorls in large part removed. The innermost septum near the center of the coil was built across the interior after the animal had constructed the hollow apex or point. It then moved along adding to the external wall of the tube, which has been destroyed and removed from this cast, and built the second septum, and so on until it reached the tenth septum. By some freak of fossilization a number of the septa beyond this have been destroyed, so that if we were to remove the fragment of the external whorl and take out the center which has just been described, this would have the exact aspect of a cast of a young shell with ten air chambers.[1] The eleventh air space or chamber being open and without divisions would then appear to be the living chamber which the animal occupied when it built the tenth septum. Normally the shell really continued to progress from the tenth septum by additions to the outer

[1] The shaded area in the center, shaped like a large inverted comma, was an open space in the living shell. This is almost invariably filled by the rocky matrix in which the shells occur and is often, as in this specimen, allowed to remain. See also figs. 4, 5, 6, on Pl. XVIII, which show the comma shaped umbilical perforations or openings left at the center through the crytoceran form of the young.

wall and put in new septa behind it, together with the connecting tube until it reached s′, and finally the last septum, l. s. This one, l. s., was really the last one built and it formed the floor of a true living chamber, l. c., formerly occupied by the animal at the time of its death and burial in the sediment of the Carboniferous period. Figs 1–2 show a similar fossil but with a longer, although still incomplete living chamber. If the external wall of shell had been preserved none of these structures could be seen. Figs. 5–7 show a fossil *Temnochilus crassus*, a shell of the same family with this external wall pre-

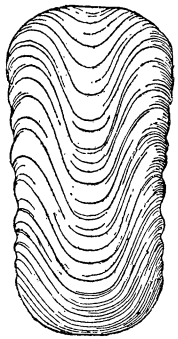


FIG. 5.

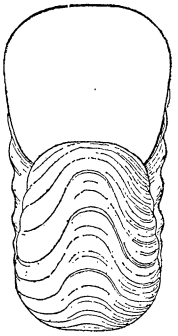


FIG. 6.

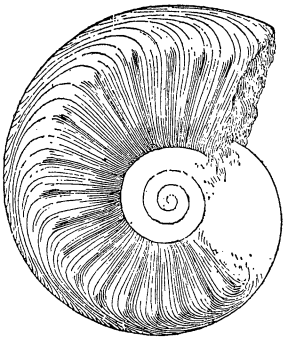


FIG. 7.

served and all these internal structures covered up. The impressed zone is the re-entrant curve shown in all these figures and especially marked in the lower outline of an outer whorl of another Carboniferous species, *Metacoceras dubium* Hyatt, fig. 8, im. z.

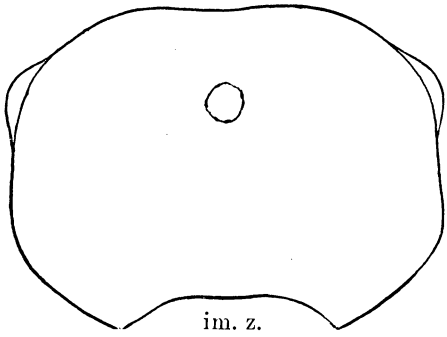



FIG. 8.

It is not necessary to go into a discussion of the details of internal structures and their relations to the impressed zone in this abstract, but it is essential to give a general description of the morphogeny of the order of Nautiloids.

This group of chambered cephalopods contains the following classes of forms: first, straight, conical shells, type Orthoceras, pl. XVIII, fig. 1; second, curved cones, Cyrtoceras, pl. XVIII, fig. 2; third, loosely coiled, open whorled cones, Do., fig. 3; fourth, coiled cones with the whorls more or less enveloping, Do., fig. 5. The fourth and fifth forms are usually included in the old genus, Nautilus. Practically, it is better to designate the first class as orthoceran, the second as cyrtoceran, the third as gyroceran, and the fourth and fifth as nautilian. In tracing genetic series through time they are found to diverge in their evolution, starting with the orthoceran and passing through parallel lines of forms, many of the genetic series having in succession cyrtoceran, gyroceran and even nautilian forms of the fourth and fifth classes. Others are not so perfectly parallel, stopping short with the cyrtoceran class of forms or the gyroceran. Many also begin with cyrtoceran shells, while others diverge from the gyroceran, and still other series have only nautilian shells of different grades of close coiling and involution.

The application of the law of repetition in heredity to the chambered shell-covered Cephalopods, shows that the straight orthoceran shells, pl. XVIII, fig. 1, were repeated in the young of the curved cyrtoceran forms, pl. XVIII, fig. 2, and these forms in their turn in the young of the gyroceran forms, pl. Do., fig. 3; and this may be seen by comparing the young or apical part of each shell represented in outline with the full grown shells of the preceding figures. The apex of fig. 2, with the whole of fig. 1; the apex of fig. 3, with the whole of fig. 2. It will be understood, of course, that the figures in outline represent full grown shells, except when otherwise explained and that they were built like the shells of figs. 1–2, by an animal living in their interiors and adding band after band of shelly matter to the exterior, but in these outlines the shell is sup-

posed to be perfect and the internal structures concealed.[2] The young of pl. XVIII, fig. 4, which represents the fourth class of forms repeats the cyrtoceran form, then curves more closely and just before it comes in contact there is a short time when it overlaps the apex without touching it. At this time it is plainly gyroceran like the whole of fig. 3. After it touches the first whorl just beyond the apex it remains in contact and the inner side or dorsum of the second or overlapping whorl begins to show a flattening as a result of this collision of the whorls. The sections of the orthoceran, cyrtoceran and gyroceran whorls show no such flattening in any of the specimens examined, although hundreds of different kinds have been studied. The sections are designated on the plate by the same letters as the supposed lines of the sections made through the tube, and although diagrammatic figures, they give a sufficiently clear general explanation of the facts observed. More specific figures could have been given in abundance and will be given in the paper now in course of preparation.

Pl. XVIII, fig. 5, shows the same phenomena as figure 4. The young is at first cyrtoceran like the adult whorl of figure 2, and open, then becomes gyroceran in curvature and finally overlaps the apex when it has arrived at the end of the first volution, but does not at first touch it. Then coming into contact it acquires a flattened area or faint impressed zone on the dorsum or inner side of the second volution as is shown in the section fig. 5c. This is similar to the section of figure 4 shown in fig. 4c′, which represents a cut through an adult whorl of the fourth class of forms. It differs only in being smaller on account of the younger stage of growth at which it occurs.

The entire series of forms from orthoceran to nautilian is more or less represented, even in the earliest period at which the Nautiloids appear, namely, in the rocks of the Quebec Group. There is, however, this qualification: the fifth class of forms, or the involute nautilian, are comparatively rare and become more abundant in successive periods. The young

[2] Except in fig. 9 in which a portion of the shell is broken away showing the cast of the interior and the sutures.

of Nautilian shells of the earlier periods are also not so closely coiled, or, in other words, remain open and similar to cyrtoceras for a longer time during their growth. This is shown by the large size of the central hole, or umbilical perforation, left in the center of full grown shells. This perforation is much larger, as a rule, in Paleozoic than in the Mesozoic forms.

In each period the genetic series or groups of nautilian forms have peculiarities of structure in the sutures, ornaments apertures, etc., by which they can be separated from each other and these peculiarities are the same as those possessed by gyroceran, cyrtoceran and often orthoceran shells which occurred often earlier in time so that one can trace each group of nautilian shells back to its ancestors through the parallel stages of evolution above described. The groups, in other words, are parallel in their morphogenesis, like two individuals of the same parents in their development from youth to old age.

In all of these cases the impressed zone originates as described above after the whorls come in contact, never before this time in the growth of any individuals. Barrandioceras is one of the most involute shells known in the Silurian, and pl. XVIII, fig. 6, gives a true sketch of this species; fig. 7, shows a section of a full grown shell with a decided impressed zone; and fig. 8, is the young. This last is a purely cyrtoceran form with a compressed elliptical section like that of fig. 7, but no impressed zone, the inner side being rounded like the diagram of Cyrtoceras, fig. 2. The impressed zone is not present in the young of Ophidioceras, the closest coiled of all these forms, nor in the young of any species of the Silurian before the whorls touch, so far as known, and all of the species likely to present this peculiarity have been investigated.

The impressed zone is also invariably lost in the oldest stage of the whorl of every individual when the whorls cease to continue to grow in contact. This condition is represented in the last part of the outermost whorl of figs. 4 and 5 in sections, figs. 4e, 5e, and in the outlines of their apertures which are elliptical. The sections represent cuts through the whorls

when, as is the case in extreme age, these cease to increase in size. As soon as this senile contraction begins to occur the sides shrink, becoming narrower, the amount of involution becomes less, and the impressed zone, shrinks in breadth as shown in the sections. When the whorl finally parts company in consequence of continued contraction the already shrunken impressed zone, figs. 4d, 5d, rapidly disappears and the apertures of such shells are frequently as round and free from indentations on the inner as on the outer side, as is shown at the free end of the figures 4 and 5.

In normally uncoiled forms, usually named Lituites, when the adult or young is coiled, and the succeeding stages, whether representing adults or old shells, are uncoiled, the phenomena are similar. The impressed zone is lost after the growth ceases to bring the whorls of the shell into contact.

The young and the adults of many of these forms have now been observed in the earliest periods and it is, therefore, obvious that during these early times the impressed zone must have been a modification of the whorl which took place in consequence of the mechanical effects produced by close coiling. This characteristic is slight when the coiling is slight and is developed in precise proportion to the increase of coiling or involution of the whorls and, on the other hand, when through degeneration due to age, or to other causes, the whorls cease growing in contact, the impressed zone gradually disappears.

Thus it always appears preceded and accompanied by an observable tendency in the mode of growth toward closer coiling and that this tendency is quite capable of producing the impressed zone can hardly be denied with any show of reason, since the charateristic disappears in proportion as the pressure is relieved through the degeneration of the powers of growth force to continue the normal rate of progressive increase of bulk in old or young or prematurely degenerate shells and in uncoiled whorls of all kinds and all ages.

The shells of Devonian series of Nautiloids have also been extensively examined, especially in the more involute nautilian forms of the genus Nephriticeras, and so far not one has been found with the slightest indication of the presence of an

impressed zone in the cyrtoceran or gyroceran stages of development. In several examples also, the disappearance of this characteristic has been observed in the last stages of old whorls. There is, therefore, every reason for regarding the impressed zone as a ctetic characteristic acquired in the later stages of growth and not hereditary so far as is known in any shells of the earlier paleozoic periods.

The same statement may also be made with regard to the majority of Carboniferous shells. There is, however, a notable exception in *Coloceras globatum* (sp. De Kon.) Hyatt, and very likely some other species of closely coiled nautilian shells. In *C. globatum* of Visé, Belgium, I found in seven specimens that the impressed zone appeared while the whorl was still in the cyrtoceran stage. Pl. XVIII, figs. 9–10, give outlines of the adult of this species, and figs. 11–12, of the young and the zone, showing that the impression appeared long before the whorls touched each other and began to assume nautilian characters. Section, fig. 13b, shows the impressed zone occurring in the cyrtoceran stage while the venter or outer side of the whorl was rounded. Such facts admit of but one explanation, namely, that in this species the impressed zone had become hereditary and was in consequence repeated at an early age, previous to the occurrence of close coiling which produced it in the ancestral forms of the same group.

There are certain correlative characters which lead me to think that this is only a partial statement and perhaps a more complete and better one would be as follows: that the impressed zone, together with a peculiar broadening out of the dorsum and helmet-shaped section of the whorl, and perhaps also certain forms of sutures occurred in the early stages of some Carboniferous species before the nautilian stage, and consequently they must have been introduced by heredity into the development of this species before the tendency to close coiling had completed the first whorl. Thus these characters, although purely ctetic in origin, were repeated before the usual conditions recurred in the ontogeny of this species which had obviously and repeatedly produced them in the nautilian forms of the earlier paleozoic and the more general-

ized genetic series of the Carboniferous. That this species, *Col. globatum*, is a highly specialized species is shown by other characteristics, especially the early inheritance of a furrowed abdomen, shown at v in Pl. XVIII, fig. 11, and a peculiar aperture.

The Triassic period is unimportant in this connection since it has but few nautilian species that are deeply involute and also sufficiently well known to throw any light upon this problem. All of the true orthoceran, cyrtoceran and gyroceran forms diminish in the Carboniferous and disappear with the Trias.

The Jura contains a considerable number of nautilian shells of different genera of which the cyrtoceran stages are sufficiently well known. *Cenoceros aratum*, of which several specimens have been studied, shows the impressed zone and correlative characters in this stage; *C. lineatum* is the same; *C. clausum*, same; *C. intermedium*, same. Pl. XVIII, fig. 14, shows the cyrtoceran stage in a shell of *C.* , with a well developed impressed zone, i. z. Endolobus is a characteristic paleozoic type and there is a single survivor of this series in the Jura, *End.* (*Naut.*) *excavatum* sp. D'Orb. It is, therefore, very interesting and instructive to note that this species has the impressed zone, according to D'Orbigny's figure, during the cyrtoceran stage. This species has a large umbilical perforation and is slower in coiling up than other Jurassic species. The evidence that the impressed zone and its correlative characteristics are inherited in most species of the Jura before the habit of close coiling could have acted upon the whorls so as to produce this modification is, therefore very general and convincing.

The leading characteristic of parallelism in all genetic series of Nautiloids is, as may be inferred from the facts cited. a tendency toward closer coiling and greater involution in the more specialized forms of each separate series and a correlative increase in the profundity of the impressed zone. When the impressed zone becomes inheritable in some closely coiled and involute specialized shells of the Carboniferous and in similar shells in about all of the genetic series of the Jura

this result is also directly connected with the observed fact of the quicker development of the coiling up tendency in the young of these Jurassic shells. This is shown by the small diameter of the umbilical perforation in the centers of the shells of the Carboniferous. It is also connected with the fact that the primitive uncoiled forms, orthoceran, cyrtoceran and gyroceran shells begin to die out in the Carboniferous and cease with the Trias as mentioned above.

This demonstration of the characters that accompany progress in close coiling, enables me to fill a gap which occurs in the evidence during the Cretaceous. In this period the existence of the impressed zone during the cyrtoceran stage of individuals has not been clearly established by observation except in two species, a form allied to *Cymatoceras pseudoelegans* D'Orbigny, from Faxoe, and *Cymatoceras elegans* from Rouen. In other shells, although a considerable number have been broken down, the state of preservation has been invariably imperfect. The coiling, however, in the young of all the shells examined is notably more accelerated than in the similar shells of the Jura, and the whorls broader and having more specialized characteristics correlative with closer coiling and the early existence of an impressed zone. It is, therefore, fair to infer that the evidence when accessible will confirm the facts observed in previous periods.

The same arguments apply also to the Cenozoics, except that in this period there is as yet no evidence of the early inheritance of the impressed zone. I have not yet succeeded with the Aturia, which is the only genus represented by favorably preserved specimens within my reach, in exposing the apex of the whorl. The shells of this period, so far as I know them, are, however, excessively involute and have exceedingly small umbilical perforations with very deep impressed zones after the whorls touch. The umbilical perforation in Aturia is in fact smaller than in any nautiloid known to me.

The imperfect evidence so far gathered in the Cretaceous, and the absence of positive evidence in the Cenozoics, does not, therefore, seriously affect conclusions reached in this paper, since these are merely gaps in the history of the evolu-

tion or phylogeny of the impressed zone; and all the correlative characteristics which accompany the inheritance of the impressed zone in the cyrtoceran stages of species which have this peculiarity have been observed to be present.

The terminal members of the Nautiloids are, of course, the existing species. *Nautilus pompilius* has been examined in a considerable number of specimens and in all of these the impressed zone and correlative helmet-shaped whorl and broad flattened dorsal side appears during the cyrtoceran stage. Pl. XVIII, figs. 15–16 are outlines of the shell of this species during the cyrtoceran stage exhibiting the helmet shaped whorl, broad dorsum, or inner side, and its impressed zone, iz. Thus, when the whorls touch, as in all the nautilian shells of the Carboniferous, Jura and Cretaceous in which the same acceleration of development also occurs, the whorl is already prepared to become involute and to mould itself more readily and rapidly over the surfaces of the apex and the side of the succeeding whorls. In other words, heredity has begun the work before the whorls touch, and before the deepening and enlargment of the impressed zone through the pressure of close coiling is begun. There are quite a number of characteristics in the species of existing Nautili which lead to the inference that they are survivors of Jurassic and generalized Cretaceous and Cenozoic forms; the size of the umbilical perforations, the smoothness of the shells, the simplicity of the sutures, and so on. These facts are of importance only in so far as they show that the existing Nautilus does not represent the acme of progress of its order but is a descendant of shells with less complicated structures than many of the genera of the Carboniferous, Jura, and Cretaceous.

## EXPLANATION OF PLATE XVIII.

### LETTERING.

a. Apex of shell. This usually bears a scar on the point, as shown in figs. 14 and 15, but this has no bearing on the question discussed, and has not been described. This also represents the youngest or cyrtoceran stage in the growth of the shell, fig. 8 being a young shell with complete living

chamber. This letter also indicates the location of the sections correspondingly lettered in the figures.

b is used to indicate the section of the cyrtoceran stage in figs. 11–13.

b′ is used to indicate the place of the sections, figs. 4–5b′, upon the whorls of figs. 4–5. They were taken through the whorl in the gyroceran stage.

c is used for the adolescent stage of growth in the whorl and the corresponding sections.

c′ is used for the full grown stage in the growth of the whorl and the corresponding sections:

d for the first part of the senile stage:

e for the final and most degenerative part of the senile stage:

i. z. for the impressed zone.

v venter or outer side of the shell, the dorsum being the inner side of the whorl.

w for the whorls, thus 1 w in figs. 3 and 4 means the end of the first whorl, 2 w the beginning of the second whorl, 3 w that of the third whorl. These letters serve to show the progressive increase in numbers of the whorls in the different classes of forms.

FIGURES.

Fig. 1. Outline of an orthoceran shell.

Fig. 2. Outline of cyrtoceran shell.

Fig. 3. Outline of gyroceran shell.

Fig. 3. Outline of nautilian shell, having a larger umbilical perforation at (a) and fewer whorls at the same age, than in fig. 5, in other words it is less tightly and completely coiled up than the class of shells represented by that figure.

Fig. 5. A nautilian shell with tighter coils than in fig. 4 and the whorls coming in contact and the impressed zone beginning at an earlier stage.

Fig. 6. Barrandioceras——(sp. Barrande) Hyatt, showing the most involute of the Silurian shells so far as known; fig. 6 is reduced in size but the section fig. 7 is natural size.

Fig. 8. A young shell of the same, natural size, with complete living chamber.

Fig. 9–10. Coloceras globatum (sp. De Koninck) Hyatt, adult. Fig. 9 has a part of the outer shell broken off showing the edges of the septal partitions (sutures) as lines on the strong cast of the interior.

Figs. 11–13. Same to show the cyrtoceran stage and section, with its impressed zone.

Fig. 14.

Figs. 15–16. Nautilus pompilius to show the cyrtoceran stage with its impressed zone.